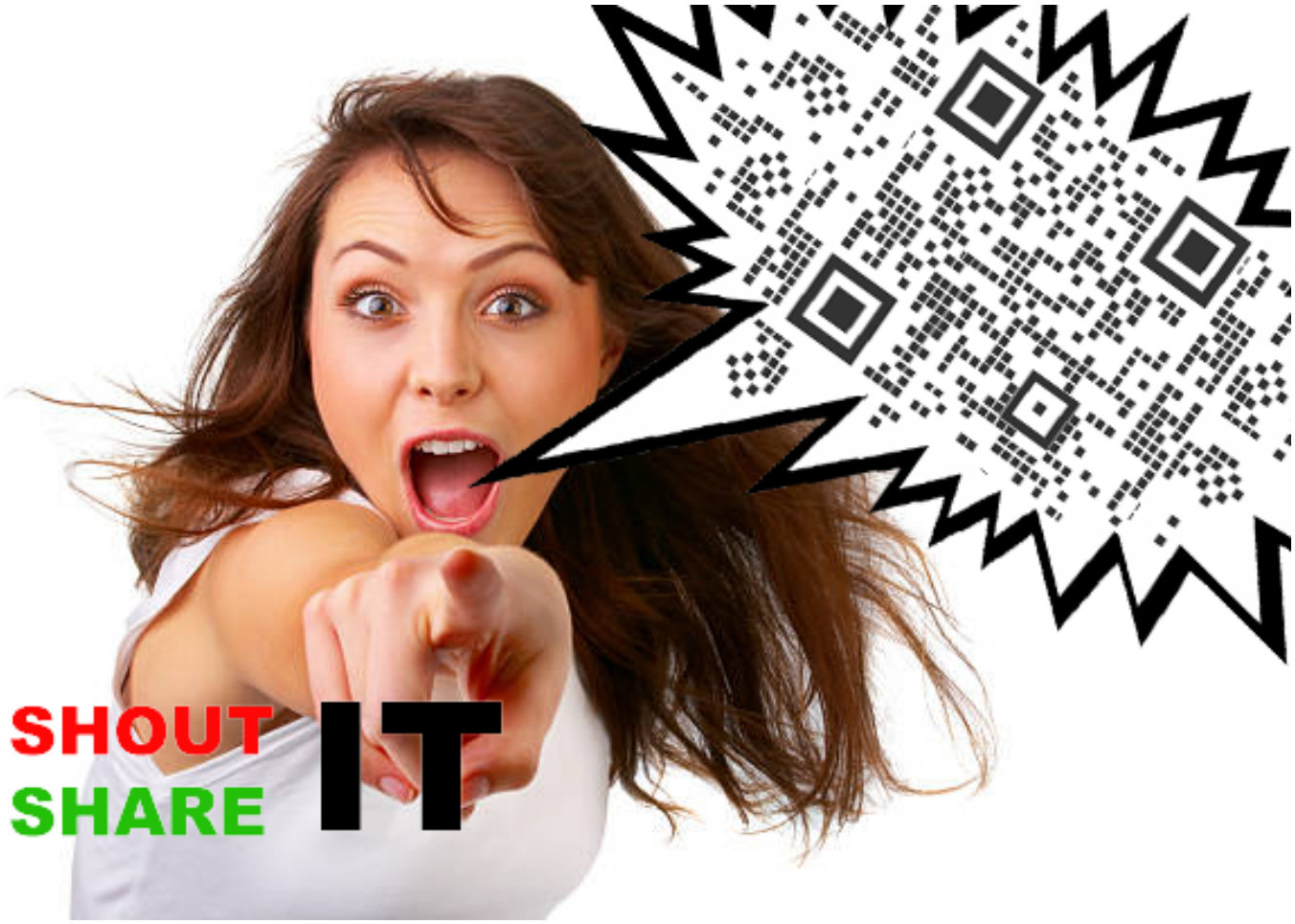
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This volume is dedicated to Dr. Rainer Zangerl

Reconstruction and Interpretation of *Brittsia problematica* D. White (Fern, Pennsylvanian)

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ABSTRACT

The complex shape of the leaf called *Brittsia problematica* suggests a floating life habit. The rachis and the pinna axes are flattened. The pinna axes have lateral lobes extending in the plane of the axes. The pinnules are lacerated and extend out of this plane. Several of the above mentioned characteristics of *Brittsia* are similar to those described by Phillips and Andrews (1968) from the fertile frond portion of *Biscalitheca*. Therefore, it becomes more likely that *Brittsia* is a coenopterid fern belonging to the Zygopteridaceae.

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INTRODUCTION

Brittsia problematica is one of the most unusual forms of sterile foliage from the Pennsylvanian. It is in part a three-dimensional frond. This fact makes its reconstruction as well as its recognition in a compression complicated.

Brittsia was first found in Henry County, Missouri, and described by David White (1899). He offered explanatory sketches along with a detailed description. Both contributions are very precise. However, he did not supply a complete reconstruction or interpretation of the function of the frond. In 1938 Němejc published an account of the *Brittsia* material found in Czechoslovakia. D. White (1899) as well as Němejc (1938) and more recent authors (Cridland, 1966; Barthel, 1968) were mainly concerned with the systematic position of *Brittsia*.

MATERIAL AND METHODS

D. White's material of 11 specimens numbered (USNM 5554 A,B; 5555 A,B; 5693; 5722 A,B; 5723; 5724 A,B; 5811) still forms the largest group of specimens and is the basis of the present study. The collection

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FIG. 1. Model of the leaf of *Brittsia problematica.*

originates from two localities in the vicinity of Clinton, Henry County, Missouri (D. White, 1899, p. 101). The material came from the level of the Jordan Coal. This name is locally used for the Rowe Coal which is stratigraphically in the middle Krebs Subgroup of the Cherokee Group, Desmoinesian Series.

A new specimen was located in the paleobotanical collection of Indiana University (specimen no. IU 68100). It came from the shale above the Indiana Upper Block Coal, Brazil Formation, Allegheny Group. The locality is the Old Glory 33 Mine, NW ¼, NE ¼, sec. 11, T8N, R6W, Coal City 7.5 Quad. The specimen is not complete but some details are well preserved.

Němejc (1938) reported specimens from three coal basins (Plzeň, Radnice, and Kladno-Rakovnik) in Czechoslovakia. There *Brittsia* occurs in the upper part of the Lower Radnice Beds and the Upper Radnice Beds. The Radnice Beds are of Westphalian C age (Havlena et al., 1968).

FIG. 2. Model of the leaf of *Brittsia problematica*. Tip of leaf.

The Rowe Coal has been correlated with the beds directly underlying the Upper Block Coal (Kosanke et al., 1960). Thus the two American occurrences are stratigraphically not far apart. The level at which they occur is about the middle part of the Westphalian. Therefore, it appears that all three occurrences of *Brittsia* are of approximately the same age.

The unusual position of the pinnules made it necessary to build a model. Only in this way was it possible to achieve a perception of the appearance of the leaf. The scale of 5:1 was used (figs. 1, 2). Two pinna axes were left bare of pinnules so that the axes might remain visible.

DESCRIPTION OF *BRITTSIA PROBLEMATICA*

Leaf more than 9 cm. long, more than 8 cm. broad, general outline elliptical or round (fig. 3); rachis flattened and 3-6 mm. broad (8-13 mm. in Czechoslovakian specimens), wavy with interrupted longitudinal striation; pinna axes in one plane with the rachis, attached $\pm 90°$ in the middle and 45° near the distal and proximal end of the rachis; pinna axes shorter near tip and base of leaf; pinna axes always form right angle with outer margin of frond (derived from specimen USNM 5722 A and 5723); $\geq$7-8 pinnae on one side of rachis (apparently more in Czechoslovakian specimen).

Pinna more than 3.5 cm. long, axis flat and 2 mm. broad, winged with rounded fleshy lobes which are up to 5 mm. broad; cicatrices protruding downward between the lobes in a funnel-shaped way. Lobes do not show vascular bundle; they are partly overlapping (fig. 4).

Pinnules about 8 mm. long and 7 mm. wide, triangular in outline, attached at one corner, distal margin with teeth, open dichotomous venation, veins 0.3 mm. broad; pinnules not in

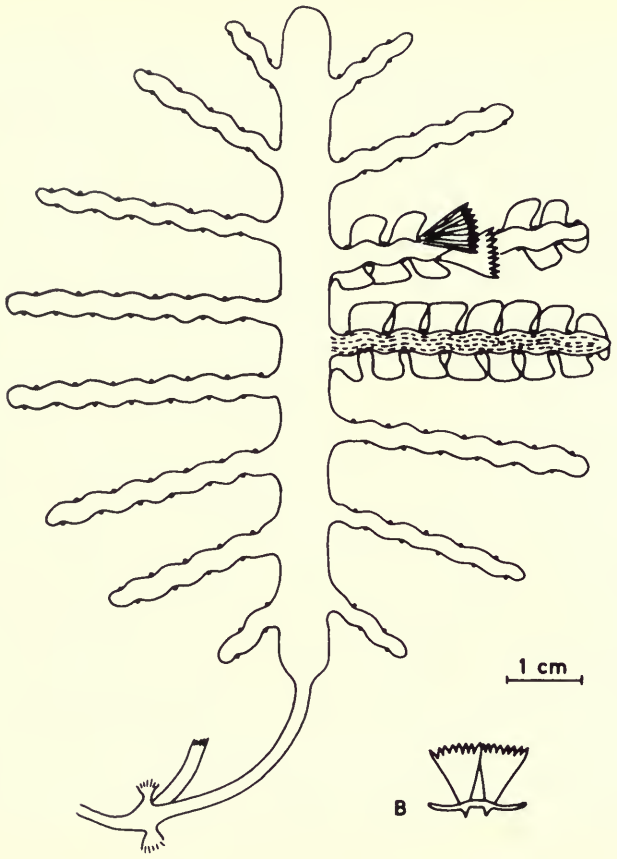

FIG. 3. Sketch of the axial system of the leaf of *Brittsia problematica*. Lateral lobes shown only on two pinna axes. Only two pinnules shown. Black dots represent cicatrices. **B**, Cross-section of a pinna. The phyllopore in the lower part of the sketch is drawn after the specimen from Czechoslovakia figured by Němejc (1938), pl. 3, fig. 3.

plane of axial system but standing up and leaning in an angle outwards, covering each other like shingles; 2 rows attached to each pinna axis; pinnules attached on axis between lobes in funnel-shaped cicatrices.

Phyllophore 1.5-2 mm. wide, furcation 25 mm. from base of leaf rachis; two lateral appendices at the point of bifurcation which could be interpreted as aphlebiae (derived from Němejc, 1938, and material in Prague).

This description is a combination and rephrasing of the descriptions given by D. White (1899) and Němejc (1938).

As D. White (1899) did not designate a holotype, a lectotype is established here. Lectotype: USNM 5772, White, D., 1899, Fossil Flora of the Lower Coal Measures of Missouri: U.S. Geol. Survey Monograph 37, pp. 98-101, pl. 48, fig. 3.

FIG. 4. Part of three pinna axes of *Brittsia problematica* with lateral lobes and cicatrices. USNM 5724; scale 5:1

DISCUSSION

The leaf of *Brittsia problematica* consists of two components which occupy two different levels (fig. 1). The flattened rachis and pinna axis together with their fleshy lateral lobes are developed in one plane. Thus the axial system alone has the appearance of a complete planar leaf (fig. 5). The pinnules were standing on the upper side forming any angle of 10 to 90° but probably around 45° before burial. In the fossilized state there are thin laminae of shale between the coaly remnants of the pinnules. As the pinnules cover each other like shingles it is impossible to expose more than one pinnule in its entirety.

The pinnules have an open dichotomous venation and a lacerated margin. These two characteristics give them an aphlebia-like appearance. There is quite a contrast between the rounded, entire outline of the lobes of the pinna axis and the lacerated appearance of the pinnules. Another significant difference exists between the wide flattened rachis (up to 13 mm. wide) and the thin (1.5-2 mm.) phyllophore (fig. 3).

The contrast between entire lobes and dissected pinnules occurs in *Brittsia* in parts of the same leaf. Such differences are known to occur in partly submerged plants between leaves in different positions. Floating leaves do have quite frequently an entire margin, while emersed leaves have often a serrate margin.

If the leaf of *Brittsia* had been floating on the water the thin phyllophore would not have been a handicap. The flattened shape of all axes does make sense in this respect and the downward warping of the lobes as well as the downward cicatrices would have increased buoyancy.

There is the possibility that the leaf of *Brittsia problematica* was either lying on the ground or on the surface of some other fern-like foliage. However, the floating frond hypothesis is favored here since the elevated position of the pinnules makes more sense if the substrate had been water.

The systematic position of *Brittsia* has been discussed by several authors. D. White (1899) listed *Brittsia* under "incertae sedis" but compared it in general shape with *Schizopteris pinnata, Androstachys frondosus,* and *Araucarites spiciformis* of Grand'Eury (1877). All these forms are considered to belong to the *Zygopteris-Biscalitheca* complex. Němejc (1938) considers *Brittsia* to be a coenopterid fern within the etapterids (=Zygopteridaceae). Cridland (1966, p. 993) mentions *Brittsia problematica* tentatively as a possible sterile foilage of *Biscalitheca.* Barthel (1968) mentions *Brittsia* in his treatment of zygopteroid compressions but gives no definitive conclusion. The general consensus seems to be that *Brittsia* is the sterile foliage of a zygopterid fern.

FIG. 5. *Brittsia problematica.* Specimen USNM 5722; scale 1:1; lectotype

In 1968 Phillips and Andrews published a reconstruction of the fructification *Biscalitheca musata,* which gives more details than any previous publication on *Biscalitheca* or similar fructifications. There are several features which are comparable to those found in *Brittsia.* The main rachis of Phillips' and Andrews' (1968, p. 104) material "is flattened in the plane of the primary pinnae, but the ultimate or secondary pinnae are directed slightly upward away from the rachis and out of the plane described by previous divisions." *Biscalitheca* has two different types of pinnules coming out of the primary pinna (called pinna in this paper). These are the stalks of the sori and the secondary pinnae (called pinnules in this paper), which project out of the plane of the frond.

It is by no means implied here that *Brittsia* and *Biscalitheca* are the same, but it can be safely said that morphological evidence indicates that *Brittsia* belongs to the Zygopteridaceae. It might even be safe to say that *Brittsia* is one of the many types of sterile foilage connected with *Biscalitheca-Zygopteris-Schizostachys*-like fructifications.

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